Dr. Morris moved to amend by striking out all after the word *Periodicals*.

Mr. Horner moved to amend by inserting after *Periodicals* the words "taken by them."

Prof. Heilprin moved to amend by inserting after *Periodicals* the words "including Transactions and Journals."

The amendments were accepted by the original mover, and the resolution, as finally amended, was unanimously adopted as follows:

Resolved, That the Secretaries be authorized to communicate with the officers of the other scientific societies and libraries in Philadelphia, for the purpose of preparing a Union List of Scientific Periodicals, including Transactions and Journals taken by them.

And the Society was adjourned by the presiding member.

The Phylogeny of the Sweat-Glands.

By Prof. John A. Ryder.

(*Read before the American Philosophical Society, October 4, 1889.*)

The suggestion of the descent of the Mammalia through a reptilian ancestry has been favorably received by many naturalists. In this connection, those singular Permian types described by Prof. Cope under the name of *Theromora* may be recalled. The *Theromora* present certain striking resemblances to the monotremes, but what their integuments may have been like in microscopic structure we shall probably never know. And it is just upon this question of integumentary structure that much of high taxonomic importance rests. Upon examining the integument of vertebrates the general plan of structure is found to be very similar in all of the orders. The main differences arise (1) through variations in the thickness of the epiblastic epidermis and the mesoblastic dermis or corium; (2) the arrangement of the connective-tissue fibres of the latter, and (3) the absence or degree of development of glands in connection with the epidermis.

The tendency of the fibres of the corium to interlace in three directions in fishes is marked, and may be best seen in selachians and chondrosteans, while it is equally striking amongst Marsipobranchii. The fibres seem to be disposed in annular layers, between which longitudinal layers are disposed, while the whole is firmly bound to the subcutaneous connective tissues by fibres which traverse the meshes of both the preceding layers, this third

class of fibres having a direction which is vertical to the outer surface of the body.

In the other groups the fibrous layer or corium departs more or less from this primitive arrangement; the type which presents the least departure from the arrangement of the elements of the two integumentary layers of fishes are the Batrachia. Above the Batrachia, the subcutaneous layer begins to show the fibres running irregularly without such an obvious arrangement of laminæ. This is the case in Reptilia, but in Aves, over the feathered areas, there is a tendency for the fibres of the corium to be disposed in coarse quadrangular or lozenge-shaped meshes, the decussations of which correspond to the points of insertion and mode of arrangement of the deeply implanted feathers.

In Mammalia there is the greatest variation in the thickness of the epidermis. In the elephant the epidermis is quite thin, but the corium in the most exposed parts is of enormous thickness and contains a great proportion of elastic fibres, that kind of tissue reaching a most phenomenal development in this form, even invading the adipose and muscular tissue in all parts of the body of the animal.

In the Cetacea and hippopotamus the epidermis is much thickened and the papillæ of the corium greatly elongated. These two forms are amongst those which depart most widely from the usual type characteristic of Mammalia, in that in the first the sudoriferous glands appear to be wanting, and the corium is rudimentary, while in the latter they are modified into the remarkable organs concerned in the secretion of the red exudation, "bloody sweat," which has been noticed by many writers, but which was never adequately studied until examined by Max Weber.*

The development of the glands of the skin, which are always in direct genetic relation with the epidermis, opens up questions of considerable phylogenetic interest, and to call attention to these is the purpose of the present note. If we tabulate the classes of vertebrates according to the degree of development of the dermal glandular organs some singular as well as interesting contrasts are brought out and clear evidence of the method of evolution of these organs is also obtained.

A.—1. The fishes (selachians, teleosts, etc.) tend to develop numerous scattered unicellular glands of the skin, as goblet cells.

These single-celled structures have doubtless multiplied side by side and given rise, first, to a pit, then by further invagination to a flask-shaped glandular appendage of the epidermis, somewhat according to the method suggested by Lang.† In this way the simplest form of epidermal gland, such as is seen in the Batrachia, may be supposed to have arisen.

It is at least suggestive that the persistence of goblet cells in the alimentary tract and bladder of some forms (the bladder being primarily a diverticulum of the intestine) is an inheritance from the gastrulated stage

* Studien über Säugethiere. Ein Beitrag zur Frage nach dem Ursprung der Cetacean. 8vo, Jena, 1886.

† Lehrbuch der Vergleichenden Anatomie, 8vo, Jena, 1888, p. 39, Figs. A, C, D, E.

of metazoan development, seen in the living Cœlenterata, in which the goblet-cell type of epidermal gland first appears. This persistence is due to the persistence of the physical conditions favoring the survival of such a primitive type of gland, the epithelium of the alimentary canal of even the highest types being constantly bathed with fluids, in much the same way as the skins of the lowest aquatic vertebrates and the cœlenterates are constantly in contact with the surrounding water.

2. The marsipobranchs are anomalous. The slime glands or lateral sacks of *Myxine*, with their singular coiled-up bodies, first described by J. Müller, are not of epidermal origin, but lie in or beneath the corium.

The representatives of the goblet cells are the refringent clavate glandular cells so numerous and embedded at various depths in the epidermis of the adult lamprey, with their narrow bases resting upon the corium. In the young lamprey these cells are superficial and rounded, occupying more nearly the position of goblet cells. The inference, therefore, is that the Kolben and Körner-zellen of the epidermis of marsipobranchs have wandered inwards from the surface into the deeper parts of the epidermis, and have been probably derived from what were primarily goblet cells.

B.—1. The Batrachia are characterized throughout by the possession of a remarkably developed system of epidermal glands. The function of these organs in batrachians is doubtless manifold, while their structure is extremely simple, being mere flask-shaped organs over most of the integument, and having a very extensive distribution, extending even over the eyelids, tympanic membrane and under surfaces of the manus and pes. The only departures from the simple flask-shaped type of the skin glands in this group is on the under surface of the pes and manus and in the parotid region of certain salamanders (*Chioglossa*, Wiedersheim). In some of these cases there is a slight tendency for these organs to become racemose; but this is rare and exceptional, just as it is rare and exceptional for the sudoriferous glands of Mammalia to become racemose, those of hippopotamus showing this tendency (Weber).

The function of the epidermal glands of Batrachia is to pour out a whitish, viscid and very acrid secretion. The inner ends of the secretory cells of the walls of the glandular sacks are sharply defined and are seperated by a very distinct outline from the mass of secreted matter contained in the follicle. The method of secretion is therefore not akin to that of the cells of a mucus gland; the nuclei of the secreting cells do not, as in the latter, occupy a quite peripheral position.

The secretion is, however, very mucus-like, as is easily learned upon handling the common frog where the skin is constantly bathed by the secretion. It is known to be also very poisonous if injected into the blood of warm-blooded animals, the secretion being also highly poisonous to other species of batrachians if injected into their vessels, death in all cases resulting in a few hours.

It is also intensely acrid in some if not in all forms; that secreted by

the skin of a living *Hyla carolinensis*, if placed upon the human conjunctiva, produces an intense burning sensation similar to and almost as uncomfortable as that produced by red pepper brought into contact with the same parts. This experiment with the secretion of *Hyla* the writer upon one occasion accidentally inflicted upon himself. The acrid and poisonous properties of the secretion are therefore also probably protective in a high degree to the various forms of Batrachia, which are otherwise but poorly provided with organs of offense and defense.

Another purpose which these glands also subserve is that of keeping the skin constantly moist, in this manner making the integument more efficient as a respiratory organ, such a function of the integument being highly developed in the Salientia.

It is not certain if these organs also serve as an excretory apparatus, but it is highly improbable that an apparatus so highly differentiated as are these epidermal glands of the Batrachia and which secrete so actively and directly to the exterior, should not also be found to serve as emunctories somewhat after the manner of the sudoriferous glands of Mammalia. I therefore regard it as highly probable that they are also excretory in the sense that they share in the process of the discharge of waste matters.

As to their structure the following may be remarked. They are obviously formed in absolute continuity with the epidermis. They lie just beneath the epidermis, or they may be said to be sessile or without any stalk-like duct leading from the saccular portion to the epidermis to the exterior. The canal, however, which passes from the gland through the epidermis has flattened cells differentiated in its walls, so that one may say the efferent duct presents the character of a canal with a wall formed of flattened elongated cells, the whole duct being embedded in the epidermis. At the point where the saccular portion of the gland and its duct join there is evidently a very gradual transition from the cells of the glandular part of the organ to those of its duct. Whether the smooth muscular fibres which run nearly parallel with each other from the point where the gland passes into the duct to the fundus of the latter are derived from the epidermis or not cannot be made out with certainty from the structure of the adult skin. These flattened muscular elements taper towards the duct and converge toward one point at their opposite ends over the inner globular end or fundus of the gland. In teased preparations the relations of these muscular fibres to the gland may be very distinctly seen, reminding one somewhat of the manner in which the curved cycle of staves forming the sides of a barrel are joined together by their edges. There is only one layer of these smooth muscular fibres, though in some cases the edges of two adjacent fibres seem to slightly overlap each other. The very intimate union of the gland, its duct and its muscular investment, and the close union of the whole to the overlying epidermis, indicate very clearly that the mode of origin of the structure is that which has already been described, viz., a simple involution of the epidermis. The only part of this whole structure the epidermal origin of which is in doubt are the

smooth and longitudinally disposed muscular fibres, though it is to be borne in mind that just beneath the closely grouped globular or flask-shaped glands there occurs the outer non-fibrous and granular layer of the corium which contains no cellular elements. This non-nucleated layer is followed by the rather thick fibrous corium, containing connective-tissue cells. This layer of fibrous matter has a horizontal disposition and the included cells are much flattened, and like the fibrous tissue are parallel to the surface. Then follows the second or deepest layer of pigment, and in this latter the principal dermal blood vascular network is embedded. This deeper vascular network, however, joins a much less developed and more superficial vascular network of capillaries, which ramifies just beneath the epidermis, their junction being effected at intervals by means of small vessels, which penetrate the inner fibrous and outer granular layers of the corium. This outer capillary plexus forms a mesh of vessels just below the epidermis. This outer plexus also forms more or less complete plexuses about the globular glands already spoken of. The blood vascular plexus is incomplete over the deeper ends of the glands, but narrow lymph channels and spaces surround them. These lymph spaces are probably continuous with the intercellular spaces between the deeper strata of epidermal cells, and communicate with the larger intercellular lymph passages which are very obvious between many of the cells of the second or penultimate layer; the direct outward communication of these wider intercellular superficial passages seems, in fact, to be shut off by the presence of the outermost layer of epidermal cells, the edges of which are closely joined together. The only remaining elements of the skin to be mentioned is the outermost or superficial layer of pigment cells just beneath the epidermis. The most superficial blood vascular plexus is in close relation to this outer stratum of pigment cells; these frequently extend over the sides of the glands immediately overlying their coat of smooth muscular cells. In densely pigmented regions the pigment cells frequently form a reticulum under the epidermis and over the glands, the processes of the cells loaded with pigment granules blending so as to produce the appearance of a fabric with irregular meshes, this meshwork being depressed at close intervals in the form of a minute reticulate sack into which a gland depends in each instance.

The walls of the glands in sections are composed of clear cubical cells containing a bright nucleus and two or more nucleoli.

This description is drawn from the appearance presented by sections of the skin of the common edible frog of the United States, *Rana catesbiana*, and from the writer's observations upon other forms; the account given applies in general terms to a great many other batrachian forms.

2. The next group (Reptilia) does not possess epidermal glands except in a few instances, over a few very limited areas of the integument. The discussion of their integument in this connection would therefore be of no interest, since the integumentary glands have for the most part been lost or suppressed.

3. In the birds, or Aves, with the exception of the oil gland on the tail, there are no integumentary glands which can be compared with those of the Batrachia.

4. In the Mammalia the case is very different, for in this group we again for the first time encounter epidermal glandular structures which may be legitimately compared with those in the Batrachia. Aside from the modifications which have resulted from the specialization of the different layers of the mammalian integument, the only difference which the sweat glands of the latter present in comparison with the epidermal glands of Batrachia are such as may be ascribed to the farther development or progressive evolution of a type of integumentary gland in all structural respects essentially similar to the skin glands of the last-mentioned group. In the next place, the majority of the Mammalia possess integumentary glands which are scattered over the whole of the body. In this respect the Batrachia and mammals are the only forms which essentially agree in the distribution of their integumentary glandular organs other than the mammary, and a few others found in the latter group. The absolute want of a generally distributed integumentary glandular system in the two great groups of Reptilia and Aves proves that the phyletic history of these two series is very old, and perhaps almost or quite coeval with that of the Mammalia. It is almost equally certain that the three series, Reptilia, Aves and Mammalia, have had a common remote aquatic ancestry, and that the oldest members of that ancestral series had the integuments defended by goblet cells, followed by a succession of forms in which flask-shaped integumentary glandular organs were developed. Are the existing Batrachia representatives of that series which possessed the simple flask-shaped integumentary glands? Were the *Theromora* provided with simple saccular integumentary glands? These are questions still to be answered. From all that we know of the integuments of the primitive types of vertebrates, we may assume, with every assurance of the legitimacy of the deduction, that both Reptilia and Aves have probably lost the integumentary glands corresponding to the sweat glands of Mammalia.

In the Mammalia the sweat glands are characterized by the differentiation of a long tubular efferent duct, which has a slightly spiral direction, which becomes more marked where the outer portion of the duct passes through the stratum corneum of the epidermis. At the other end, the simple tubular and properly glandular portion of the gland usually lies in a close coil invested by a plexus of capillary vessels. Or this deeply-lying glandular portion may not be so closely coiled, but extend as open loops or irregular bends amongst masses of areolar and connective tissue, as may be well seen in the sweat glands of the ball of the foot of the domestic cat, though here, as in other forms, the relation to the blood vessels is the same. In all these cases, however, there is essentially the same structure, namely, a lining secretory epithelium and an investment of longitudinally disposed unstriped muscular fibres, an arrangement which can be compared only with the arrangement of the tissues making up the far simpler integumentary glands of the Batrachia.

If we now turn to the Batrachia in quest of integumentary glands which bear a still greater resemblance to the sudoriferous or sweat glands of Mammalia, we find them on the balls of the toes and integumentary thickenings of the footpads of certain *Salientia*. Integumentary glands with a long duct and a short tubular secretory portion have been described by F. Leydig* from the tips of the digits of Bufo, Pelobates, etc. The structure of these organs, moreover, corresponds exactly to that of a very immature or embryonic sweat gland which has become provided with a duct or has acquired a lumen. They have the same lining of secretory cells in the deeper glandular portion covered by longitudinal muscular fibres. They have already acquired a long non-glandular efferent duct, which is evidently homologous, so far as structural details are concerned, with the efferent ducts of the sweat glands of mammals.

In the light of all the evidence now at our command, the following conclusions seem to me to be warranted :

1. That the integumentary glands of Batrachia and the sweat glands of mammals have had at least a common ancestral origin.

2. The method by which an integumentary gland as simple as that of the Batrachia might become converted into a sudoriferous gland would involve, in the first place, a comparatively slight change of function, and, in the second place, simple elongation in the direction of its own axis and the differentiation of an outer non-secretory portion serving as a duct and a deeper glandular portion. Some of the steps in this process have been alluded to, and it only remains for us to suppose that as a result partly of the great thickening of the epidermis in mammals that the efferent ducts have acquired greater length while the simple tubular glandular portion has simply grown in length and become pressed into a close coil, as its functional importance became greater.

3. That the Theromora may have possessed integumentary glands, seems not unlikely from the fact that they are believed by Prof. Cope to be the most batrachian-like reptiles.

4. It is equally probable that, with the change of habit from that of a water and moisture-loving animal to one of terrestrial habits, the primary form of integumentary gland would undergo important functional changes or adaptations, as great or greater than the change in form of the gland.

5. The principal change in the character of the integumentary glands is in their form. They pass gradually from a rounded globular form in lower types to a more elongate tubular and even much coiled form in the higher types, while preserving essentially the same morphological structure. The writer therefore believes that there is no escape from the conclusion that the comparatively complex sudoriferous glands of higher types have arisen by differentiation from the simpler defensive or poison-secreting, integumentary glands of some lower type in which they closely resembled those of the living Batrachia.

* Ueber den Bau der Zehen bei Batrachiern und die Bedeutung des Fersenknochens. Morph. Jahrb., II, 1876, pp. 165–196, Pl. viii–xi.